

HOW WELL DO ECOSYSTEM-BASED PLANNING UNITS REPRESENT DIFFERENT COMPONENTS OF BIODIVERSITY?

Ralph Mac Nally

Section of Ecology, School of Biological Sciences, Monash University 3800, Australia

Corresponding author. Phone: 61 3 9905 5642; Fax 61 3 9905 5613; e-mail:

Ralph.MacNally@sci.monash.edu.au

Andrew F. Bennett

School of Ecology and Environment, Deakin University, Clayton 3168, Australia

Geoff W. Brown, Linda F. Lumsden

Arthur Rylah Institute, Department of Natural Resources and Environment, 123 Brown St, Heidelberg,
3084 Australia

Alan Yen, Simon Hinkley, Peter Lillywhite and Darren Ward

Environment Program, Museum Victoria

GPO Box 666E, Melbourne 3001, Australia

Abstract. There are many proposals for managing biodiversity by using surrogates, such as umbrella, indicator, focal and flagship species. We use the term *Biodiversity Management Unit* for any ecosystem-based classificatory scheme for managing biodiversity. The sufficiency of Biodiversity Management Unit classification schemes depends upon: (1) whether different biotic elements (e.g. trees, birds, reptiles, etc.) distinguish between Biodiversity Management Units within a classification (i.e. *coherence within classes*); and (2) whether different biotic elements agree upon similarities and dissimilarities among Biodiversity Management Unit classes (i.e. *conformance among classes*). Recent evaluations suggest that biodiversity surrogates based on few or single taxa are not useful. Ecological Vegetation Classes are an ecosystem-based classification scheme used as one component for biodiversity management in Victoria, Australia. Here we evaluated the potential for Ecological Vegetation Classes to be used as Biodiversity Management Units in the Box-ironbark ecosystem of central Victoria, Australia. Eighty sites distributed among 14 Ecological Vegetation Classes were surveyed in the same ways for tree species, birds, mammals, reptiles, terrestrial invertebrates and nocturnal flying insects. Habitat structure and geographic separations also were measured, which, with the biotic elements, are collectively referred to as variables. Less than half of the biotic element–Ecological Vegetation Class pairings were coherent. Generalized Mantel tests were used to examine conformance among variables with respect to Ecological Vegetation Classes. While most tests were not significant, birds, mammals, tree species and habitat structure together showed significant agreement on the rating of similarities among Ecological Vegetation Classes. In this system, use of Ecological Vegetation Classes as Biodiversity Management Units may account reasonably well for birds, mammals and trees, but reptiles and invertebrates would not be accommodated. We conclude that surrogates will usually have to be augmented or developed as hierarchies to provide general representativeness.

Key words: Biodiversity, box-ironbark woodland, conservation planning, ecoregions, habitat structure, Mantel test

Running headline: Biodiversity management units

INTRODUCTION

The conceptually straightforward task of managing biodiversity is in practice a difficult proposition. This is due to the resources needed for: (1) establishing existing patterns; (2) planning; (3) on-going monitoring; (4) on-the-ground management; and (5) compromises needed in largely human-dominated agricultural or forestry landscapes (Landres et al. 1988; Launer and Murphy 1994; Lambeck 1997; Simberloff 1998; Fleishman et al. 2000). The expense and time required for such tasks (especially points 1–3) has led to the suggestion that surrogates for biodiversity be used. Flagship, umbrella and indicator taxa are some of the surrogates suggested for efficiently meeting conservation objectives by using single or several species instead of whole biotas (see Andelman and Fagan 2000 for definitions and an even more extensive list of surrogate classifications). Whichever taxon is used, it is meant to be a surrogate that is representative of patterns of biodiversity across the study domain (Margules and Pressey 2000).

Surrogate systems: Biodiversity Management Units

Limitations to the usefulness of single or small numbers of species as surrogates (Andelman and Fagan 2000) have led to the suggestion that more general ecological categorizations be considered for biodiversity management. These frequently relate to ecosystems or plant communities (Faith et al. 2001b). Margules and Pressey (2000) commented that higher-order surrogates may be useful because they represent integrated aspects of ecological processes better than arbitrary species subsets. Moreover, in many parts of the world, vegetation mapping may be the only reasonably detailed ecological information available reflecting patterns of biodiversity (e.g. Faith et al. 2001a).

As one example, Ricketts et al. (1999) analysed ecoregions of North America for the degree of correspondence among distributions of nine taxa (birds, mammals, butterflies, amphibians, reptiles, land snails, tiger beetles, vascular plants, trees). Ecoregions are relatively coarse biogeographic

divisions reflecting broadly similar environmental conditions and natural communities (Ricketts et al. 1999). A similar scheme exists for Australia (Interim Biogeographic Regionalisation for Australia or IBRA; Thackway and Cresswell 1995).

We use the term *Biodiversity Management Unit* to refer to an ecosystem-based classification, usually of easily recognized or mapped entities, that might be used in managing biodiversity based upon an ensemble of biotic, climatic and physical (e.g. landform) characteristics. Ecoregions or IBRA units are possible Biodiversity Management Unit classifications.

We believe that there are two requirements for classifications to be useful as Biodiversity Management Units: (1) for each taxonomic group (e.g. birds), the assemblages of species in sites belonging to the same Biodiversity Management Unit class should be more similar to one-another than to assemblages drawn at random from all Biodiversity Management Unit classes (Fig. 1a); and (2) among taxonomic groups (e.g. mammals and birds) there should be a broad agreement between similarities and dissimilarities of Biodiversity Management Unit classes (Fig. 1b). If assemblages of mammals are relatively similar between two classes, then assemblages of birds also should be relatively similar. Moreover, if bird assemblages between two classes are relatively dissimilar, then mammalian assemblages also should be relatively dissimilar. We refer to (1) as *coherence within classes*, and to (2) as *conformance among classes*. A similar idea to (2), congruence, has been used in several other studies to represent a spatial correlation of richness or endemism among diverse taxa (e.g. Howard et al. 1998; Ricketts et al. 1999). A useful classification scheme that is effective as a basis for Biodiversity Management Units will be coherent within classes and conformant among classes.

Fig. 1

Ecological Vegetation Classes

Here we test the degree to which there is coherence within and conformance of biotic elements among Ecological Vegetation Classes. These classes have been proposed as a possible basis for large-scale land management (see below). Ecological Vegetation Classes are defined as: “one or more floristic communities which exist under a common regime of ecological processes and which are linked to broad landscape features. The similarity of environmental regimes is manifested in comparable life forms, genera and vegetation structure” (Muir et al. 1995, p. 9). Ecological Vegetation Classes are a finer-scale unit of classification than IBRAs or ecoregions. Given that all vascular plants are used in two-way tables to construct Ecological Vegetation Class classifications, trees, of which typically there are < 5 species per site, tend to have little influence on the classifications. Therefore, we consider tree-species composition distinctly from Ecological Vegetation Classes within this study.

Ecological Vegetation Classes as Biodiversity Management Units?

The principal land-management agency responsible for biodiversity management in the State of Victoria, Australia, is the Department of Natural Resources and Environment (DNRE). This agency has proposed using Ecological Vegetation Classes as part of a framework for biodiversity management. For example, in specifications for biodiversity conservation for the Forest Management Plan for the Central Highlands of Victoria, the primary management guideline included these protection objectives: (1) 30% retention of any Ecological Vegetation Class occupying > 1% of public land; (2) 30%-90% retention of any Ecological Vegetation Class occupying 0.1–1% of public land; and (3) 90% retention of any Ecological Vegetation Class represented on < 0.1% of public land (Anon 1998).

The potential advantages of using Ecological Vegetation Classes are clear: extensive field mapping and relationships with climatic, edaphic and topographic data allow the generation of Ecological Vegetation Class maps for the entire region and make comparisons of alternative management scenarios more straightforward. If Ecological Vegetation Classes are an effective Biodiversity Management Unit basis, then the potential gains in management efficiency would be very great. If all Ecological Vegetation Classes were sufficiently well covered in a reserve or protected system, then there would be high confidence that regional biodiversity would be adequately represented (Pressey and Nicholls 1989; Margules and Pressey 2000). This clearly need not preclude requirement for additional provisos (e.g. availability of large, old trees for hollow-nesting animals; special consideration for problematic taxa; seral stages in forests and woodlands).

In this paper, we consider whether the Ecological Vegetation Classes of the Box-ironbark forests and woodlands of central and north-eastern Victoria, Australia, might be an effective Biodiversity Management Unit classification by analysing coherence and conformance of birds, mammals, reptiles, terrestrial invertebrates, nocturnal flying invertebrates and tree species. Box-ironbark Ecological Vegetation Classes mostly fall within just one of the 80 IBRA units in Australia (Victorian Midlands). In the proposed management plan for public lands in this system, Ecological Vegetation Classes have been suggested for conservation management in a similar way to that in the Central Highlands (ECC 2000).

We have detailed data for diverse biotic elements collected on the basis of sites within Ecological Vegetation Classes, so we were able to use these data to explore the adequacy of units—like Ecological Vegetation Classes—for biodiversity management. If classifications such as Ecological Vegetation Classes are to be useful as Biodiversity Management Units, then coherence of each taxonomic group should be significant for each Ecological Vegetation Class, and there should be

broad agreement among all taxonomic groups *vis-à-vis* how Ecological Vegetation Classes are ranked in term of similarities. If these conditions are satisfied, then the use of Ecological Vegetation Class-like classifications would be a helpful framework within which to manage biodiversity. Few studies have a similar concentration of systematic data collection for a variety of taxa at the same sets of locations (although see Howard et al. 1998).

STUDY SITES

The Box-ironbark system of north-central Victoria, Australia, lies to the north of the Great Dividing Range (GDR) in a broad band from the south-west (Stawell 37°06' S 142° 52' E) to the north-east (Albury-Wodonga 36°08' S 146° 09' E) of the state. The area included is just over 3×10^4 km², of which 437,000 ha is public land (14.3%) (ECC 1997). A total of 454,000 ha is still wooded (ca 14.8%), of which 71.8% is public land.

Eighty sites were included in the study, which was designed to provide base-line information on the fauna of the Box-ironbark system at one point in time (mid-1990s) for future evaluation of the efficacy of changes in management practices (Bennett et al. 1999). The approximate areas, descriptions, numbers of study sites and abbreviations used for each of 14 Ecological Vegetation Classes are listed in Table 1. While there was a general attempt to stratify randomly numbers of sites as a function of the relative area of each Ecological Vegetation Class, there were some necessary deviations from this policy. Certain Ecological Vegetation Classes (e.g. Heathy Dry Forest) were so extensive relative to the smallest Ecological Vegetation Classes that a truly random stratification could not be produced, while some very small Ecological Vegetation Classes had particular management interest, and so, were included for this reason.

Table 1

FIELD METHODS

Faunal surveys were undertaken at all 80 sites, each 1 ha (250 m × 40 m) in extent. Sites were located across the entire geographic range of the Box-ironbark region. All survey sites were within large tracts of natural vegetation on public land to reduce possible impacts of habitat fragmentation (Mac Nally et al. 2000, Mac Nally and Brown 2001). The principal variables used in the study are listed in Table 2.

Table 2

Site measurements

Twenty-one structural variables were measured for each site, and these comprised the *habitat-structural* data set (Mac Nally et al. 2000). Numbers, species and sizes of all trees were recorded over the 1 ha extent of each site, as were densities of shrubs, logs, stumps, hollows, etc. Cover variables (e.g. grass/forbs, bare-ground, litter) were measured for each site on the basis of five plots, each 20 m in diameter (a total of 0.157 ha). One plot was randomly positioned within each 50 m section of the 250 m-long transect to ensure representation of the transect as a whole. As appropriate, data were expressed as densities (e.g. shrubs), areas or volumes ha^{-1} , or % cover. Basal coverages of all tree species irrespective of the size of trees (> 10 cm diameter at breast height over bark) were computed, forming the basis for the *tree-species* data set.

Geographic separations. Latitudes and longitudes of all sites were determined and these were used in conjunction with the Unix *Perl* script *dist* (courtesy of D. Kindred, Department of Computer Science, Carnegie-Mellon University, Pittsburgh USA) to compute the geographic separations of pairs of sites.

Faunal surveys

Birds. Diurnally active birds were surveyed by undertaking transect censuses of 20 min duration on two occasions in each of the austral spring/summer (October-December 1995) and austral winter (June-July 1996). For birds alone, the study plots were 2 ha—extending the width of the 250 m transects to 80 m. In each season, one census was conducted in the morning (commencing after dawn but before 1030 hours) and one later in the day (on a different day). Thus, each of the 80 sites was surveyed four times. The observer moved slowly along the midline of the 250 m-long transect and recorded all birds seen or heard ahead of the observer within the 2 ha survey site.

Mammals. Mammals were surveyed by using a range of complementary techniques at each site. This was necessary because of the diverse range of habits of mammals from almost strictly arboreal (possums) to aerial (bats) to ground-dwelling (antechinuses). The suite of techniques was applied with equal intensity at all sites so that sampling was unbiased with respect to sites. Nocturnal, arboreal mammals were detected by using spotlight transects at night, with each site searched on three occasions. Hair-sampling tubes (Suckling 1978) were employed to detect small ground-dwelling and scansorial mammals. Ten small tubes were nailed to trees (ca 2m above ground) and three large funnel tubes (Faunatech, Melbourne, Australia) were located on the ground at each site. Samples of hair collected in tubes were identified following the techniques described by Brunner and Coman (1974). Bats were surveyed over the austral summer peak activity period by using two techniques (Duffy et al. 2000). A harp trap (Tidemann and Woodside 1978, with modifications by Austbat Pty Ltd, Melbourne, Australia) was erected at each site for two successive nights, and an ultrasonic bat detector (*Anabat* detector and delay switch, Titley Electronics, Ballina, New South Wales, Australia) linked to a tape recorder was used to detect calls throughout a single night. Calls were identified by using *Anabat V* and *Analook* software (Titley Electronics) based on comparisons with a reference library of species calls from the same area (Duffy et al. 2000). Indirect observations of mammals, based on skeletal material, diggings or faeces, were also systematically made at each site by searching along the transect.

Reptiles. Reptiles were surveyed by conducting transect counts (50 m \times 10 m) and active searches (25 m \times 10 m), with a total of eight censuses at each site (four of each type). Each transect was randomly situated within the 1 ha area. For transect counts, the observer moved slowly along the transect and recorded any reptiles observed, while active searches involved deliberate searching for reptiles under logs or rocks, behind bark and in other microhabitats. Pitfall trapping was undertaken

at a subset of 40 sites in nine Ecological Vegetation Classes. Use of pitfall traps is logistically demanding (see Mac Nally and Brown 2001), precluding its use in all 80 sites. Pitfall trapping involved use of ten 20 l buckets, spaced at 10 m intervals, which were buried in the ground to their rims. A Y-shaped fibreglass/flywire drift-fence, 40 cm high and held vertically erect by metal pegs, was placed over the center of each bucket. Daily (five days per site) monitoring of pitfall traps was carried out in November 1995 and March 1996 and individuals captured were identified and then released unharmed.

Nocturnal flying invertebrates. Nocturnal flying invertebrates were sampled in conjunction with bat trapping by using a light trap for two successive nights. Invertebrates were attracted to a vertically directed cone of light powered by a 12 V light source positioned 0.5 m above ground. Specimens were sorted to ordinal level and counted.

Terrestrial invertebrates. Ground-dwelling invertebrates were sampled at each site by using a line of 10 pit-fall traps (500 ml plastic jars, 70 mm diameter) spaced at 5 m intervals. Pitfall traps were left in place for one month in the austral spring of 1995 (October–November). Ethylene glycol was used as a preservative in each trap. Individuals were sorted to ordinal level and counted.

STATISTICAL ANALYSES

For each faunal group and tree species, the species-by-sites matrix was converted into a similarity-among-sites matrix by using the Bray-Curtis index (Minchin 1987). Gross differences in composition among Ecological Vegetation Classes were examined by using analysis of similarity (ANOSIM, Carr 1994). The ANOSIM procedure involves Monte Carlo randomization of the observed similarity data to assess whether the observed pattern of dissimilarities and similarities among pre-defined groups is unlikely by chance alone. Thus, if there are two groups for example, a test statistic (R , Clarke 1993) is computed to summarize the observed pattern of dissimilarities among these pre-

defined groups. Then, the observed dissimilarities are randomly allocated to two pseudogroups of equal sizes to the real groups, the global test statistic computed for this random arrangement, and a statistical sampling distribution for the test statistic, R , is generated by performing the randomization many times (see Clarke 1993). The ANOSIM procedure has a related analysis—SIMPER—that identifies those species contributing most to the similarities within groups and to differences between groups. This works on the basis of computing the total contributions of species to the Bray-Curtis similarities (within groups of sites) or dissimilarities (between groups of sites). The PRIMER software package (Carr 1994) was used to undertake the ANOSIM and SIMPER calculations. Similar analyses were undertaken for habitat structure.

Analytical procedures and protocol

Stage 1. For each variable listed in Table 2, an ANOSIM was performed to determine whether there was a non-random arrangement among Ecological Vegetation Classes.

Stage 2. The SIMPER program was used to determine two values for each variable: (1) within-Ecological Vegetation Class similarities; and (2) among-Ecological Vegetation Class dissimilarities. The former were used in Stage 3, while the latter were utilized in Stage 4.

Stage 3. (Coherence within Ecological Vegetation Classes). By using the complete similarity matrix based on 80 sites (where possible, see Reptiles below), the statistical significance of the within-Ecological Vegetation Class similarity was computed by using resampling. For example, if there were five sites for a given Ecological Vegetation Class and thus ten combinations of site pairs, ten pair-wise similarities were randomly selected from the 3160 (i.e. ${}^{80}C_2 = 80!/(78!2!)$) similarities and the mean similarity computed. This was repeated 1000 times to produce a distribution of possible mean similarities from random sets of 10 similarity indices. If the observed value was greater than the largest 2.5-percentile of these 1000 means, then the coherence of faunal constitution within

the Ecological Vegetation Class was regarded as statistically significant. If, the observed value was less than the smallest 2.5-percentile, then the coherence was regarded as non-random in such a way that sites within the Ecological Vegetation Class had faunas more different than expected by random arrangements.

Stage 4. (Conformance among Ecological Vegetation Classes). In Stage 4, correspondence among different taxa (and geographic separations and habitat structure) was tested by using the among-Ecological Vegetation Class dissimilarities computed in Stage 2. First, those taxa in which quantitative density estimates were available (birds, invertebrates) were compared with presence/absence-transformed data to determine whether the same signal arose if densities or presence/absence were used. This is important because only presence/absence data were available for certain taxa, such as mammals, due to the range of sampling methods required to characterize adequately those elements of the fauna. Density and presence/absence information produced similar results so among-Ecological Vegetation Class dissimilarities were based on densities where possible (e.g. birds, invertebrates).

Second, to determine whether there were agreements among faunal groups and habitat variables, the among-Ecological Vegetation Class mean dissimilarities were used in a generalized Mantel-test procedure. The usual Mantel statistic is (see Legendre and Fortin 1989, p. 135):

$$\mathfrak{R} = (1/(N-1)) \sum_i ((x_i - \bar{x})/s_x)((y_i - \bar{y})/s_y), \quad (1)$$

where there are N dissimilarities (= all combinations of pairs of Ecological Vegetation Classes, in this case ${}^{14}C_2 = 14!/(12!2!) = 91$), and x and y designate different aspects to be assessed (e.g. x = birds and y = mammals). Barred terms are means and s terms are standard deviations. The Mantel procedure involves randomizing the orders of the x and y vectors and producing a distribution of possible \mathfrak{R} -values based on the observed data, against which the observed statistic is tested.

A generalized Mantel statistic was constructed based on (1):

$$\mathfrak{R}_G = (1/(N-1)) \sum_i \prod_{j=1 \dots Q} ((x_{ij} - \bar{x}_j)/s_j) \quad (2)$$

where Π indicates the product over a number of variables. This is a simple generalization of (1) in which the x and y are designated as x_1, x_2, \dots, x_Q , where there are Q variables. Again, the Q variables can be randomized and a distribution of possible \mathfrak{R}_G statistics (typically 1000) produced, against which the observed values can be assessed. The number of variables ranges from two to as many as necessary (here seven). Standardized Mantel statistics (\mathfrak{K} s) also were calculated; these are: $\mathfrak{K} = (\mathfrak{R}_{G,obs} - \bar{\mathfrak{R}}_G) / s_{\mathfrak{R}_G}$. These values indicate how many standard deviations the observed value was above or below the mean randomized value.

We invoked the principle of hierarchy (Chevan and Sutherland 1991) to assert that significant agreement among variables in a given set requires that all of the combinations in the hierarchy are statistically significant. For example, a four-variable combination (e.g. birds, mammals, habitat structure and nocturnal flying invertebrates) might produce a significant \mathfrak{R}_G statistic. However, this may be driven by one strong pair-wise agreement (e.g. habitat structure and nocturnal flying invertebrates) rather than a four-variable agreement *per se*. Thus, the hierarchy principle requires that all pair-wise, three-way and the four-way tests (in this case) within the hierarchy are significant before concluding that there is a four-variable agreement. Note that as one is interested in positive relationships (i.e. conformance), tests are one-tailed so that significance is regarded as when the observed statistic exceeds the upper 5-percentile.

Notice that the Mantel test-statistics (1, 2) involve linear correlations only. To guard against non-linear relationships among dissimilarities (e.g. between habitat structure and tree species variables, which did occur), all dissimilarities within variables were rank-transformed. Upon inspection, this method successfully eliminated non-linearities.

RESULTS

Basic findings and ANOSIMs

Birds. There were 101 species of native birds recorded during the survey, 20 of which were found at only one site each. The distribution of bird species among Ecological Vegetation Classes was significantly non-random (Table 3).

Mammals. Twenty-four species of native mammals were found in this project, ten of which were bats. Two species of mammals were found at only one site each. Mammals also were distributed non-randomly among Ecological Vegetation Classes (Table 3).

Reptiles. Nineteen species of reptiles were detected overall, five of which were located at only one site each. The analysis for reptiles was restricted to only those sites at which pitfall traps were used. This resulted in just nine of the Ecological Vegetation Classes being included because several of the geographically smaller Ecological Vegetation Classes were not sampled by using pit-fall-traps. There was no evidence of differences in the reptilian fauna among those nine Ecological Vegetation Classes (Table 3).

Nocturnal flying invertebrates. There were 20 orders represented in the nocturnal flying invertebrate data set with 25,000 specimens in total. Lepidoptera constituted 36.0%, 30.5% were dipterans and 20.1% were Coleoptera. The assortment of invertebrates trapped by using light-sources at night was significantly non-random (Table 3).

Terrestrial invertebrates. Forty-seven orders of invertebrates (308,000 specimens) constituted the data for terrestrial invertebrates. The only orders with = 1% were Hymenoptera (58.6%), Coleoptera (22.2%), Diptera (7.4%), Hemiptera (4.3%), Araneae (2.9%) and

Thysanoptera (1.0%). There was no difference overall among Ecological Vegetation Classes (Table 3).

Table 3

Tree species. The distribution of tree species among Ecological Vegetation Classes of sites was significantly non-random using basal-area coverages (Table 3).

Habitat-structure. The distribution among Ecological Vegetation Classes of sites was significantly non-random when habitat-structural variables were considered (Table 3).

Coherence within Ecological Vegetation Classes

Birds. The avifaunas of sites in ten of the Ecological Vegetation Classes were significantly more similar to each other than among the same numbers of sites drawn randomly from the 80 sites (Table 4). The other Ecological Vegetation Classes (GHHW, MSSW, HHW, PGW; see Table 1 for explanation of abbreviations) had apparently random assemblages of birds and did not appear to be recognized as coherent units by the birds. While the average Bray-Curtis similarity among all pairs of sites (3160 pairs) was just 0.158 (Table 3), the four LRGW sites averaged 0.634 similarity, most likely because of the numerical dominance of one species (Noisy Miner *Manorina melanocephala*).

Table 4

Mammals. Sites from only six Ecological Vegetation Classes were significantly coherent (Table 4); the remainder appeared to be random collections of mammalian species drawn from box-ironbark Ecological Vegetation Classes. The two PGW sites were remarkably similar (0.917) compared with the overall mean similarity for mammals of 0.668. Eleven species were recorded at both PGW sites, only the Inland Broad-nosed Bat *Scotorepens balstoni* was found at just one of the

pair, while twelve other species, found in other Ecological Vegetation Classes, were not recorded in either site.

Reptiles. The highest-quality data were derived from the sites at which pit-fall trapping was used, thus restricting analyses to nine Ecological Vegetation Classes and 38 sites (exclusive of the two pit-fall sites with no records). Three of the Ecological Vegetation Classes had coherent reptile assemblages: GHHW, MSSW and ATHW (Table 4).

Nocturnal flying invertebrates (ordinal resolution). Sites from five of the Ecological Vegetation Classes were significantly coherent (Table 4). Given an overall mean pair-wise similarity of 0.365, the highest mean within-Ecological Vegetation Class similarities of 0.740 (LRGW), 0.736 (SRW) and 0.685 (GSM) were highly coherent.

Terrestrial invertebrates (ordinal resolution). Only three of the Ecological Vegetation Classes showed significant coherence (0.796—GHHW, 0.769—ATHW, 0.827—LRGW), which exceeded the overall pair-wise mean similarity of 0.599 (Table 3). Curiously, the four CGW sites were significantly less similar than expected among any random selection of four sites from the 80 sites overall (Table 4). In CGW sites, hymenopterans ranged between 42–98% of individuals, dipterans constituted 0.6–39% and hemipterans 0.1–11%. The sites were widely separated geographically. These disparities contributed to the abnormally large within-Ecological Vegetation Class dissimilarities.

Tree species. Ten of the 14 Ecological Vegetation Classes were significantly coherent (Table 4). While mean pair-wise similarity was 0.129, some Ecological Vegetation Classes had within-Ecological Vegetation Class mean similarities exceeding 0.7 (SRW–0.844, MSSW–0.719).

Habitat structure. Eight of the Ecological Vegetation Classes were significantly coherent (Table 4). Average site-pair-wise similarity was 0.545. Highest structural similarity was in the SRB sites (0.893). All four sites had substantial low-shrub (< 2 m; mean 58%), high-shrub (> 2 m; 62%) and fine-litter (73%) coverage, low canopy coverage (12%), and low tree heights (< 5 m).

Summary. Outcomes of coherence tests indicated that across all variables listed in Table 4, there was significant coherence in 45 cases, significant incoherence in one and random distributions in 47 cases. This suggests that trees, some faunal elements and habitat structure are not, in general, strongly differentiated in similar ways among Ecological Vegetation Classes. However, ten of the 47 random cases involved Ecological Vegetation Classes sampled in just two sites (GHW and PGW) so that there was probably little prospect of discerning significance in these cases.

Mantel tests for conformance among Ecological Vegetation Classes

Twenty-three of the 120 combinations were highly intercorrelated based on rank-order transformations of the among-Ecological Vegetation Class similarities (Table 5). Exclusive of combinations involving geographic separations, 20 of 57 combinations of biotic variables were significantly correlated. The three most-pronounced pair-wise correlations had $N > 5$: habitat structure vs tree species (Fig. 2a), habitat structure vs mammals (Fig. 2b) and tree species vs birds (Fig. 2c). The six-variable combination involving just biotic elements (habitat structure, tree species, birds, mammals, nocturnal flying invertebrates, terrestrial invertebrates) was significant.

Geographic separation was rarely correlated with dissimilarity patterns of the other variables (Table 5). Both mammals and nocturnal flying invertebrates were related to geographic separations (i.e. Ecological Vegetation Classes that were further apart tended to have more dissimilar assemblages of these two groups). Although mammals and nocturnal flying invertebrates also agreed on similarities and dissimilarities among Ecological Vegetation Classes (Table 5), mammals, nocturnal

flying invertebrates and geographic separation did not form a ‘hierarchy of conformance’ because the three-way test was clearly non-significant ($\kappa = 0.074$).

Table 5, Fig. 2

Conformances among two of the three strongest relationships were weakened by several seemingly aberrant points (see Fig. 2b, c). The sixth most-similar pair of Ecological Vegetation Classes (HHW, PGW) based on habitat structure had the 90th most-similar mammalian assemblages. This pair also was tenth most-similar in tree species (sharing high proportions of Yellow Box and Grey Box). Six species were found only in PGW sites, four species only in HHW sites, while seven species were found in both (another seven were found in neither). Given the high average levels of similarities between sites in mammals (Table 3), these differences between HHW and PGW sites are striking. A knot of points in the tree species–birds plot indicates pairs of Ecological Vegetation Classes with relatively similar tree species yet relatively divergent avian assemblages (Fig. 2c). The pairs involved are MSSW with LRGW, CGW and ATHW, LRGW with BIF and ATHW, and GHW with GHHW.

Eleven of the 23 generalized-Mantel statistics that were significant were in a hierarchy consisting of habitat structure, tree species, birds and mammals. Only one of the twelve constituents of that hierarchy was not significant (habitat structure, tree species and mammals), suggesting that there was substantial agreement among these four elements given their conformance of similarities and dissimilarities among Ecological Vegetation Classes. One significant five-fold combination was a superset of the hierarchy, including terrestrial invertebrates. However, this was most likely driven by the strong mammal–terrestrial invertebrates ($\kappa = 3.262$) and habitat structure–terrestrial invertebrates ($\kappa = 3.425$) relationships because other combinations involving terrestrial invertebrates (including them with habitat structure *and* mammals, $\kappa = -0.146$) were not significant.

Summary. Multiway Mantel analyses indicated that there is probably just one conformance hierarchy of variables within the seven measured: habitat structure, tree species, birds and mammals. The seven-variable test produced a statistic close to zero ($\mathfrak{N} = -0.164$).

DISCUSSION

Conservation ecologists have seen the evolution of the biodiversity-surrogate concept from ideas based on single or small sets of taxa (umbrellas, indicators and flagships; Andelman and Fagan 2000 considered 14 variations) through to more inclusive concepts based on whole-biota or ecosystem classifications, such as ecoregions (Ricketts et al. 1999). Almost all analyses from the extremes of single species through to ecoregional analyses show that surrogates do not provide whole-biodiversity representation. Our analyses were pitched at a level between those extremes, essentially at vegetation-based classes within an ecoregion (or equivalent). Moreover, our study is among very few that provides information for diverse faunal elements that was collected consistently at all the same sampling locations within potential Biodiversity Management Unit classes (although see Howard et al. 1998). We now consider some of the implications, limitations and conclusions of our results.

Ecological Vegetation Classes as Biodiversity Management Units in the Box-ironbark System

Many of the Ecological Vegetation Classes do not appear to be recognized as distinct units by faunal elements (i.e. many do *not* have coherent faunas). Reptiles are so scantily distributed that little can be said of their relationships to different Ecological Vegetation Classes. There are wide disparities among taxa in mean similarities among all site-pairs (Table 3). For example, the mean value for birds was 0.158 and for mammals 0.668, indicating greater spatial differentiation of avifaunas than of mammalian assemblages.

The principal test of the utility of Ecological Vegetation Classes as Biodiversity Management Units lies in the conformance measures, which indicate that only one hierarchy, consisting of four variables (i.e. birds, mammals, habitat structure and tree-species), appears to be of potential use. Neither terrestrial nor nocturnal flying invertebrates conformed consistently with that foursome. The

four-variable hierarchy consisting of birds, mammals, trees and habitat structure indicated a broad conformance in rankings, which suggests that these elements of the biota might be managed within a Biodiversity Management Unit-framework based on Ecological Vegetation Classes. Of course, classifications based on tree species and upon habitat structure might be expected to conform, so that the three-variable hierarchy is of more critical significance in the context of biodiversity management. We have had responses to our analyses by workers intimately involved in the development of biodiversity management plans (e.g. R. Loyn, Victorian Department of Natural Resources and Environment). Comments included that conformance between birds, mammals and trees may be potentially useful because these three taxa are of most pragmatic interest to management. From this perspective, the possible use of Ecological Vegetation Classes as Biodiversity Management Units in the Box-ironbark system may hold some promise, although invertebrates would not be adequately represented in such a scheme.

This may be a more general problem than just for the system considered here. For example, Kerr (1997) used a geographic approach and reached similar conclusions to us. He quantified species-richness and endemism of mammals and selected orders or families of invertebrates based on $2.5^{\circ} \times 2.5^{\circ}$ and $2.5^{\circ} \times 5^{\circ}$ quadrats tiling North America. While endemism correlated well with species richness within taxa, patterns among taxa, and among orders within taxa (e.g. carnivores and insectivores), were generally weak. Kerr (1997) also showed that by using a gap analysis based on carnivores—a typical surrogacy approach—just 43.5% of the invertebrates he considered would be protected (not significantly different from random reserve selection). Kerr mentioned that his relatively coarse, areal approach left out considerations of local detail of habitats and species distributions within the large quadrats. Our study, which is intimately connected with habitats and species

distributions, nevertheless comes to many of the same conclusions (see also Ricketts et al. 1999; Andelman and Fagan 2000; Fleishman et al. 2001).

We have not considered alternative Biodiversity Management Unit classifications in this paper. Other schemes are possible. For example, the Ecological Vegetation Classes may be grouped together into coarser units such as ‘broad vegetation types’ (ECC 1997). Different results may emerge from such an analysis, but this is beyond the scope of the current paper to consider further, especially as study-site selection was so contingent upon Ecological Vegetation Classes (e.g. stratified sampling) in this study. It is also possible that the range of alternative habitat types within our study was comparatively narrow, and that a broader geographic range may exaggerate differences in faunal elements in such a way as to make discrimination and conformance between Biodiversity Management Unit bases more obvious (see Mac Nally et al. 2000, Sect. 5.2). Such scale-related issues clearly warrant attention.

Data quality

Tests for conformance, in particular, are necessarily indirect because they are based on the calculation of among-Ecological Vegetation Class, Bray-Curtis dissimilarities that have been rank-transformed. While indirect, this does not indicate that the approach is deficient but rather that the concept of using surrogates for biodiversity (indicators, umbrellas, ecoregions, Ecological Vegetation Classes) is conceptually simple but difficult to frame correctly for tests of the hypothesis.

One major difficulty is differences in levels of taxonomic discrimination and confidence associated with different faunal or floral elements. Birds were identified to species and there are often reasonable estimates of density. Surveys of mammals and reptiles rely on a range of taxon-specific methods and so, it is often not possible to produce single density estimates. Invertebrate data were

restricted to ordinal discrimination—most of the invertebrates are undescribed to species—but with abundance data.

The reliability of the derived data for all of these faunal elements differs markedly. For example, reliability of reptile surveying was clearly limited by the logistic feasibility of using pit-fall traps (Mac Nally and Brown 2001), which, when used, greatly increased the site-specific species richness. It is well known that more surveys will continue to accrete species to faunal lists, especially for birds (e.g. Colwell and Coddington 1994; Mac Nally and Watson 1997; Peterson and Watson 1998), so that any survey program will be incomplete. It is also likely that the invertebrate surveys may be subject to great lability that we were unable to address within this study; the laboratory processing of the invertebrate surveys undertaken for this study (one season, ordinal level) took ca 4 person-years. Therefore, we emphasize that even in a program as comprehensive as ours, the quality of the data available for hypothesis testing probably will vary greatly among taxonomic elements. The indirect paths by which those tests are made may, of course, contribute to a weakening of signals if they occur.

Whither surrogacy concepts?

In many parts of the world there are few resources and little expertise to conduct the kind of study undertaken here (Berger 1997; Margules and Pressey 2000; Faith et al. 2001b). However, we have seen that as the simplest kinds of potential management bases (e.g. single surrogate species) have not delivered under scrutiny (Andelman and Fagan 2000), greater inclusiveness has been invoked (e.g. broad trophic groups such as mammalian carnivores, Noss et al. 1996, Kerr 1997; focal-species, Lambeck 1997; ecological vegetation classes, the present paper; ecoregions, Ricketts et al. 1999). An increasing number of studies find a lack of agreement or congruence among very diverse taxonomic elements, such as work in Britain (Prendergast et al. 1993), Africa (Howard et al.

1998) and North America (Lammert and Allan 1999; Ricketts et al. 1999; Fleishman et al. 2001). This means that single surrogates, even those based on higher-order units such as ecoregions or Ecological Vegetation Classes, in most cases will not be representative of patterns of biodiversity in the sense of Margules and Pressey (2000).

Probably very few researchers and managers expect a miracle solution—a ‘one scheme fits all’ scenario. However, if certain biotic elements form hierarchies with significant conformances, then management may depend at least partially upon the Biodiversity Management Unit classification for biodiversity planning. This may leave out a number of taxa, and one suspects these taxa are the ones often excluded from consideration in large-scale management plans (e.g. invertebrates exclusive of butterflies). However, this may not necessarily invalidate the use of Biodiversity Management Unit classifications because the existence of certain cross-taxonomic agreements may significantly reduce the complexity of planning, allowing development of more specific plans for taxa not covered by the main thrust of the Biodiversity Management Unit classification (e.g. Faith et al. 2001b). For example, variation in invertebrate assemblages may be at such a small scale that even sites within Ecological Vegetation Classes differ as much as sites in different Ecological Vegetation Classes. At scales larger than Ecological Vegetation Classes, reptiles perhaps might be more strongly differentiated at the level of broad vegetation types, which is another layer of classification used by management agencies in Victoria. These observations suggest a hierarchical approach that needs further development (see e.g. Wickham et al. 1997).

Conclusions

What would be the effect of basing conservation planning on the system of Ecological Vegetation Classes in the Box-ironbark region? First, there is a reasonable expectation that much of the flora would be adequately accommodated by using Ecological Vegetation Classes because

patterns of floristic variation underlie the Ecological Vegetation Class scheme. On the surface, it also seems possible that the Ecological Vegetation Class scheme might be refined by taking into account whether elements of the fauna (e.g. mammals, terrestrial invertebrates) distinguish between certain Ecological Vegetation Classes sufficiently to warrant recognition of some of the Ecological Vegetation Classes as distinct entities. This may simplify the classification. We have also seen a reasonable correspondence between birds, trees and mammals in relation to their relative rankings of similarities and dissimilarities among Ecological Vegetation Classes, which may underlie a potential common planning scheme. However, while conformances are significant, coherences generally do not correspond well among these three taxa—birds, trees and mammals are together coherent biota in only four of the 14 Ecological Vegetation Classes (HDF, ATHW, LRGW, CGW; Table 4), which collectively cover < 20% of the extant forests. The pattern of coherence among Ecological Vegetation Classes is strikingly similar between habitat structure and birds, suggesting that birds collectively are influenced strongly by the differences in habitat structure that typify different Ecological Vegetation Classes. Reptiles and invertebrates do not show strong patterns of coherence or conformance. These results suggest that while Ecological Vegetation Classes may be used as planning units *in lieu* of very detailed information of all biodiversity components, their use is unlikely to produce the representative result that is one of the two main objectives of systematic conservation planning (Margules and Pressey 2000). Worse still, none of these analyses have even addressed the problem of persistence, which Margules and Pressey (2000) argued to be the second pillar of successful conservation planning. Use of single surrogates or classification schemes is unlikely to satisfy the explicit conservation objective of representing overall patterns of biodiversity. Hierarchies of classifications and special provisions for certain taxa will be needed to augment broader planning bases. Such a requirement has *de facto* recognition in the recommendations of the Environment Conservation Council in Victoria for the Box-ironbark system. Special provisions have been made to

represent areas with large old trees, gullies and drought refuges, hollow-dependent fauna, and known sites used by rare taxa in the proposed reserve system (ECC 1997).

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Table 5 Combinations showing significant conformance among Ecological Vegetation Classes based on Mantel tests (standardized Mantel statistics, \mathfrak{N}).

\mathfrak{N}	Combination
5.550	Habitat structure, Tree species
5.256	Habitat structure, Mammals
5.144	Tree species, Birds
4.234	Tree species, Mammals
3.932	Habitat structure, Tree species, Birds, Mammals
3.855	Habitat structure, Birds
3.425	Habitat structure, Terrestrial invertebrates
3.415	Habitat structure, Tree species, Mammals, Terrestrial invertebrates
3.262	Mammals, Terrestrial invertebrates
2.918	Nocturnal flying invertebrates, Geographic separation
2.850	Mammals, Geographic separation
2.689	Tree species, Birds, Mammals
2.627	Habitat structure, Tree species, Birds, Mammals, Nocturnal flying invertebrates, Terrestrial invertebrates
2.591	Habitat structure, Tree species, Birds
2.334	Mammals, Nocturnal flying invertebrates
2.317	Habitat structure, Tree species, Mammals, Nocturnal flying invertebrates,

	Terrestrial invertebrates
2.297	Terrestrial invertebrates, Geographic separation
2.248	Habitat structure, Birds, Mammals
2.232	Habitat structure, Tree species, Birds, Mammals, Terrestrial invertebrates
1.968	Birds, Mammals
1.905	Tree species, Birds, Mammals, Terrestrial invertebrates
1.883	Tree species, Birds, Mammals, Nocturnal flying invertebrates
1.748	Habitat structure, Birds, Mammals, Terrestrial invertebrates

FIGURE LEGENDS

Fig. 1 Conceptual requirements for classification units that would be suitable as Biodiversity Management Units: (a) coherence—in ordination space (e.g. multidimensional scaling), classes segregate together indicating greater-than-expected similarity within classes; (b) conformance—mean similarities between classes ranked similarly by different biotic elements, in this case, birds and mammals.

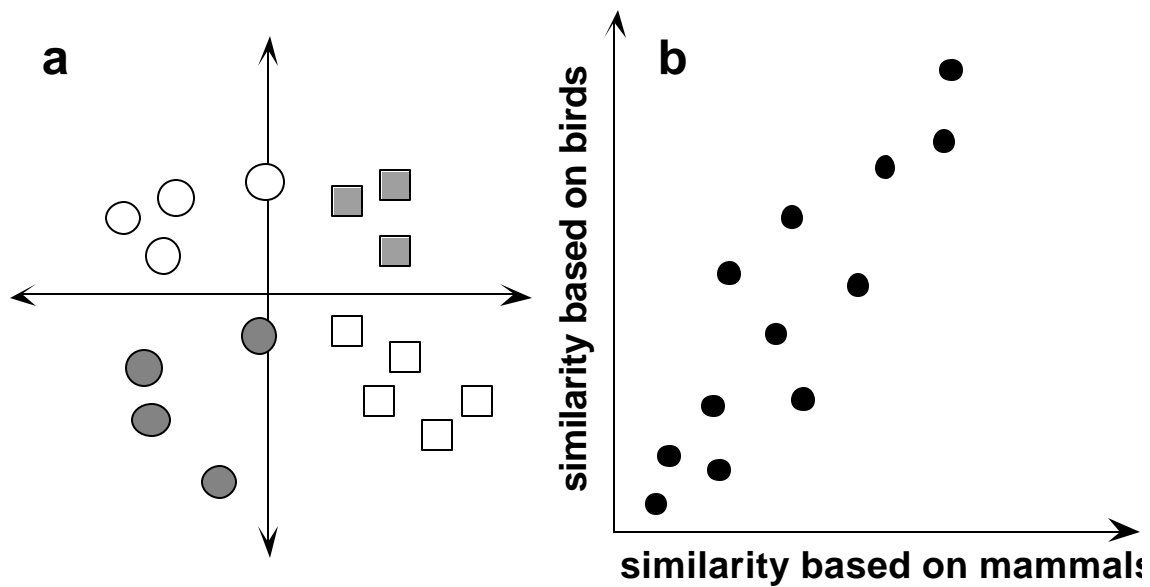


Fig. 2 The three pair-wise combinations having the strongest rank-order conformance between variables ($\mathfrak{K} > 5.0$). (a) Habitat structure (ordinate) vs tree species (abscissa); (b) Habitat structure (ordinate) vs mammals (abscissa); and (c) Tree species (ordinate) vs birds (abscissa). Lines are simple regression.

